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Using biophysical modelling and population genetics for conservation and management of an exploited species, *Pecten maximus* L.

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Abstract

Connectivity between populations is important when considering conservation or the management of exploitation of vulnerable species. We investigated how populations of a broadcast-spawning marine species (scallop, *Pecten maximus*) that occur in discrete geographic locations were connected to each other. Population genetic insights were related to the outputs from a three-dimensional hydrodynamic model implemented with scallop larval behaviour to understand the extent to which these areas were linked by oceanographic processes and how this was altered by season and two contrasting years that had strongly different average temperature records (warm vs cold) to provide contrasting oceanographic conditions. Our results span from regional to shelf scale. Connectivity was high at a regional level (e.g. northern Irish Sea), but lower at scales >100 km between sites. Some localities were possibly isolated thus dependent on self-recruitment to sustain local populations. Seasonal timing of spawning and inter-annual fluctuations in seawater temperature influenced connectivity patterns, and hence will affect spatial recruitment. Summer rather than spring spawning increased connectivity among some populations, due to the seasonal strengthening of temperature-driven currents. Furthermore, the warm year resulted in higher levels of modelled connectivity than the cold year. The combination of genetic and oceanographic approaches provided valuable insights into the structure and connectivity at a continental shelf scale. This insight provides a powerful basis for defining conservation management units and the appropriate scale for spatial management. Temporal fluctuations in temperature impact upon variability in connectivity, suggesting that future work should account for ocean warming when investigating population resilience.

KEYWORDS
biophysical modelling, connectivity, fisheries management, genetics, marine protected areas, scallop, spatial management

1 | INTRODUCTION

1.1 | Connectivity in marine systems

Connectivity within meta-populations drives population dynamics and persistence (Botsford & Hastings, 2010; Hanski, 1998). Thus, connectivity networks provide essential knowledge about the appropriate scale to focus conservation and management within the context of an ecosystem-based approach to management. Extended larval phases of several weeks for marine species can potentially link populations hundreds of kilometres apart, thereby underpinning the connectivity between populations. Connectivity within a meta-population will be important in the temporal recruitment patterns of exploited populations (Gimenez et al., 2019). However, in many cases, larvae do not always realise this dispersal potential (Bowen et al., 2006; Jones et al., 2005; Shanks, 2009). In order to understand connectivity for marine species that have a planktonic larval stage, it is essential to understand the biophysical interaction between larval behaviour, isolation by distance and oceanographic processes (Gaines & Bertness, 1992).

Dispersal of larvae away from coastal spawning locations is affected strongly by tidal currents that vary due to topographical effects. In a net sense, tidal currents tend to retain larvae in-shore in bays and estuaries (Pingree & Griffith, 1979; Robins et al., 2012), or in recirculating eddies that form off headlands and islands (Mann & Lazier, 2006; Neill & Scourse, 2009). Offshore tidal motions are more oscillatory, however, larval dispersal is influenced by wind-driven and density-driven currents that are controlled by weather patterns and seasonal cycles (Schultz et al., 2011; Seigel et al., 2008). Summer heating and stratification can form oceanographic fronts and gyres (Horsburgh & Hill, 2003; Simpson & Hunter, 1974), which may act as physical barriers to larval transport (Gilg & Hilbish, 2003) or, conversely, direct larvae along conduit pathways (Robins et al., 2013). Dispersal patterns can be modulated by rare and severe wind and wave conditions, potentially leading to the establishment of new communities which have no clear connection at other times (Hartnett et al., 2007; Monzón-Arguello et al., 2012). In this way, physical oceanographic processes underpin larval dispersal pathways—the boundaries of which are modified by timing of spawning, larval behaviour and pelagic larval duration.

Larval dispersal or local retention can form complex patterns that cannot be predicted solely from consideration of pelagic larval duration (PLD) (Cowen et al., 2006; Paris et al., 2007). Thus, interdisciplinary approaches are required, integrating larval behaviour, oceanography and genetics, to understand the spatial scales at which larval dispersal occurs. These approaches are fundamental to understand the appropriate scales at which spatial conservation through networks of marine protected areas or fisheries management regimes should be developed.

1.2 | Genetic measures of connectivity

Gene flow is restricted under conditions of low connectivity between populations. In turn, genetic drift may lead to divergence in allele frequencies within a population. Demographic evolutionary forces can be detected using neutral markers and used to infer population isolation or connectivity. Due to the low levels of migration needed to genetically mix or homogenise populations (Crow & Kimura, 2009) and the possibility of indirect connectivity through stepping-stone dispersal, genetic data on its own will tend to overestimate dispersal distance for a single generation (Shanks, 2009): Significant genetic differentiation in temporally stable populations *does* represent low demographic connectivity, which occurs at a scale that is highly significant in the context of fisheries and conservation management. However, genetic homogeneity does not necessarily equate to high demographic connectivity as it can be achieved by demographically low levels of gene flow. Therefore, genetic approaches provide a broad-scale view of connectivity and the largest scale at which management should be considered.

1.3 | Biophysical modelling of larval dispersal and connectivity

Process-based models that simulate ocean circulation coupled with particle tracking algorithms that track virtual-larvae trajectories from source to sink are widely used tools in marine ecology research (e.g. Cowen et al., 2006; Nicolle et al., 2013, 2016). Such biophysical models have been used in conjunction with genetic studies of meta-populations (e.g. Coscia et al., 2012, 2020; Gormley et al., 2015). Biophysical models will predict a range of plausible connectivities, for a specific period and given sufficient information on larval behaviour; although validation is challenging since larvae are too small to track. However, similarities between the genetic structure and modelled connectivities can provide extra confidence in the outcomes from both methodologies.

1.4 | Study species: Pecten maximus

Here, we use a commercially important scallop (*Pecten maximus*, referred to as scallop from hereon in) as a model broadcast-spawning marine invertebrate for investigating connectivity using both genetic and biophysical approaches. Scallop are broadcast-spawning hermaphrodites that have a planktonic larval phase of typically 21 days (in warm waters) to in excess of 50 day (in colder waters) (Beaumont & Barnes, 1992). Scallop are an important, commercially exploited species, found in European waters from Norway to Spain. Landings of all scallops (of which *P. maximus* make up the majority) in the UK peaked at around 54,000 tonnes in 2012 but have been falling since then to levels similar to 2008 at 29,000 tonnes in 2019 (MMO, 2019). The value of this fishery has remained much more stable over the same time period with the landings in 2012 worth £68.4 M and in 2019 worth £63.2 M. Due to their commercial importance, locations of significant adult populations are reasonably well defined by fishing activity. Previous work on the genetic structure of scallop has shown mixed results. The first published population genetic work

on the scallop used allozyme loci and studied scallops from 13 sites around the UK and France, but failed to show any differentiation among sites (Beaumont et al., 1993). Following this work, evidence of genetic differentiation between Norway and pooled UK samples (primarily from the Irish Sea and the Western English Channel) was identified also using allozymes (Ridgway et al., 2000). Mulroy Bay, an enclosed sea loch in Ireland, has been shown to differ from the rest of the UK using both mitochondrial DNA and Randomly Amplified Polymorphic DNA markers (RAPD) (Heipel et al.,. ,,1998, 1999; Wilding et al., 1997), and that a site to the east of the Isle of Man was distinct from the western sites (Heipel et al., 1998, 1999). The same mitochondrial study also suggested that Plymouth was distinct from the Irish Sea samples but there was a strange result in that the RAPD markers showed high similarity between Plymouth and the northern most Isle of Man sites but not with the southernmost ones. More recently, microsatellites have been used to further investigate the genetic structure of these scallops with variable results. Overall, studies suggest a generally homogeneous population around the British Isles, English Channel and the Atlantic coast of France, with Norway showing significant differentiation (Handal et al., 2020; Hold, 2012; Morvezen et al., 2016; Szostek, 2015). However, there is also evidence of some chaotic genetic patchiness (Hold, 2012) and temporal instability (Handal et al., 2020). Biophysical modelling of scallop larvae trajectories has suggested that the mean dispersal distance is highly variable depending on the origin leading to variable connectivity (Handal et al., 2020; Nicolle et al., 2016), even at relatively small spatial scales, creating a mismatch between modelling and genetics.

1.5 | Study aims

We combine genetic information on population structure with insights from a three-dimensional biophysical model of the northwest European shelf sea, allowing comparison of genetic and larval dispersal modelling approaches at a range of spatial scales and under a range of reproductive and environmental scenarios (cold and warm years). The study aimed to define the spatial scales at which populations are connected. This could provide insights on the most effective spatial scales for networks of marine protected areas and fishery management for *P. maximus* in northwest Europe, an example of a species with prolonged planktonic dispersal stages in a shelf sea environment. We also aimed to investigate the effect of variable reproductive and environmental scenarios on appropriate spatial management.

2 | MATERIALS AND METHODS

Pecten maximus, a hermaphroditic broadcast-spawning scallop was used as the study organism for the genetic and oceanographic simulation. The study region stretches across the northwest European shelf, covering most of the northerly range of *P. maximus* (Figure 1). The PLD ranges from 21 days in warm waters to over 50 days in cold waters, with larval behaviour varying through development from upwards swimming to the surface, alternating upwards swimming and sinking and extended periods towards the sea floor.

2.1 | Genetic methodology

2.1.1 | DNA Extraction and microsatellite genotyping

Pecten maximus tissue samples were collected from 24 sites from across Europe (Figure 1) between 2009 – 2014 and consisted of a range of overlapping age groups. Samples were stored in 90% ethanol. DNA was extracted using CTAB extraction buffer and phenol-chloroform (see Appendix S1). Eleven microsatellites were genotyped of which eight loci were from Hold et al. (2013) (PMNH 9, 11, 59, 60, 68, 70, 73 and 75) and three were taken from Watts et al. (2005) (List15-004, list15-008, list15-012). Microsatellites were amplified using three multiplex polymerase chain reactions (PCRs) (Table S1). PCR products were resolved on an ABI 3130XL sequencer using the LIZ 600 size standard. Genemapper® (Applied Biosystems) software was used to size alleles.

2.1.2 | Population structure

A full investigation of loci and population characteristics such as Hardy–Weinberg Equilibrium, null alleles and Linkage Disequilibrium can be found in Appendix S1. To calculate genetic differentiation as pairwise F_{ST} values, we used GenAlEx v6.501 (Peakall & Smouse, 2006). A Principle Coordinate Analysis (PCoA) in GenAlex v6.501 was then used to visualise populations contributing most to the overall genetic structure within the F_{ST} matrix. A power analysis was carried out using POWSIM (Ryman & Palm, 2006) to identify the power at which various F_{ST} values were detectable by our suite of markers with a significance >0.05 (burn-in = 1000; batches = 100; iterations = 1000; Ne = 10,000; t = 0, 10, 17, 20 and 200; 1000 runs). Correction for multiple testing was achieved using the False Discovery Rate (Benjamini & Hochberg, 1995).

2.1.3 | Biophysical modelling

Circulation over the northwest European shelf seas was simulated using the three-dimensional Regional Ocean Model System (ROMS; Shchepetkin & McWilliams, 2005); see Figure 1. The model has been validated for the region (see Robins et al. (2015) for details), producing errors in elevations of less than 8% and in tidal velocities of less than 14%—equivalent to less than 1 cm/s. This level of uncertainty is considered small for dispersal studies, especially since the validation encountered a number of high-velocity sites in the Irish and Celtic Seas. Further, the simulated sea surface temperatures compared

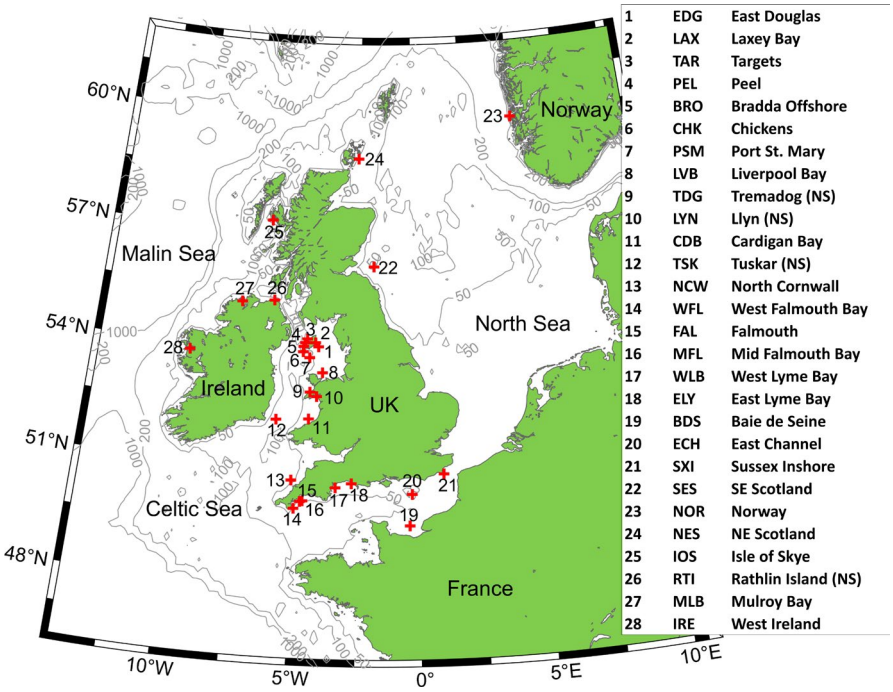

FIGURE 1 Map showing the 24 sampled scallop sites. Site codes: EDG-East Douglas, LAX-Laxey Bay, TAR-Targets, PEL-Peel, BRO-Bradda offshore, CHK-Chickens, PSM-Port St. Mary, LVB-Liverpool Bay, CDB-Cardigan Bay, NCW-North Cornwall, MLB-Mulroy Bay, IOS-Isle of Skye, IRE-West Ireland, FAL-Falmouth, WFL-West Falmouth Bay, MFL-Mid Falmouth Bay, WLY-West Lyme Bay, ELY-East Lyme Bay, ECH-East Channel, SXI-Sussex Inshore, BDS-Baie de Seine, SES-SE Scotland, NES-NE Scotland, NOR-Norway

very well to daily and seasonal fluctuations measured at Port Erin, Isle of Man (Port Erin Marine Laboratory, University of Liverpool), with an overall root mean squared error during the two simulations of less than 0.5°C. Qualitatively, the model was also compared with the Atlantic Margin Model (AMM15) setup of the NEMO ocean model (v.3.6) (for a detailed model description see Graham et al., 2018), showing very similar evolution of sea surface temperatures and development of the key tidal mixing fronts mentioned above. The model simulated the spawning season for scallops: April to September (Hold, Murray et al., 2013; Mason, 1958). Two contrasting years were simulated: a cold year (1986) and a warm year (2003), defined as minimum and maximum monthly averaged sea surface temperatures (SST) respectively, measured between 1954 and 2005 at Port Erin, Isle of Man (Port Erin Marine Laboratory, University of Liverpool). We chose typically cold and warm years to represent a maximal range in potential larval dispersal patterns, since the representative years of the samples ranged over a decade (six sampling years and of a range of age groups). As well as being impractical to simulate 3D ocean circulation over decadal scales with a spatially high-resolution (0.87–1.38 km) model, extreme cold and warm years are expected to represent a maximal range of residual flows and hence dispersal. This was confirmed by Coscia et al. (2020), who conducted similar particle tracking simulations over several years (practical in this case since the domain was smaller—Irish Sea only), showing variability in dispersal between years that was similar to that simulated in this study. During the simulated cold year (1986), stratification caused by solar heating during the summer was relatively weak, hence, the associated density-driven currents that are key to larval transport were also weak. For example, the residual flows associated with the Western Irish Sea gyre, the Celtic Sea front and Irish coastal current, and the Ushant and English Channel fronts (Holt & Umlauf, 2008). In contrast, the warm year produced stronger density-driven circulation along these features that has the potential to greatly affect larval transport. Therefore, we consider ranges in the hydrodynamics caused by seasonal and inter-annual effects, which could be a significant control on larval dispersal and connectivity (Neill & Hashemi, 2013).

Simulated 3D velocities and diffusivities were used to drive a Lagrangian particle tracking model (PTM), whereby virtual-larvae particles were transported according to the ambient circulation and mixing, together with the migration behaviour of scallop larvae. The simulated velocities incorporated diffuse mixing. Additional mixing of particles at sub-grid scale was also accounted for using a random walk algorithm described in Robins et al., 2013. Dispersal from the 24 genetically sampled scallop populations, plus four more commercially important populations within Europe (see Figure 1) were simulated. Each release area was 2 km^2, although scallop beds cover a greater area in many cases. Each release comprised 100,000 particles spawned during 01–05 April, 01–05 July and 01–05 September, for both cold and warm years, the rationale being that this strategy statistically represents a wide range of possible trajectories for this region (Robins et al., 2013). Cohorts were tracked with behavioural traits determined from observational and laboratory studies of *P. maximus* (Appendix S2). Our behaviour model incorporates the likely range in larval duration, which is temperature driven, by allowing up to 50 days for settlement. However, we did not vary the timing of spawning to reflect fluctuations in temperature as this would require extensive field-based validation across a range of regions which was beyond the scope of our study. Modelling results focus on the potential connectivity between the 24 sampled and four additional populations across northwest Europe. Particles that travelled within 10 km of a settlement site during the pediveliger stage were counted (once only). To measure connectivity or local retention, the percentage of released particles arriving at a paired site was calculated (i.e.

the number of simulated particles arriving at a destination site divided by the number of particles released from a spawning site).

2.1.4 | Drivers of genetic differentiation

The relationship between oceanographic distance (shortest sea-distance between two points calculated in R; script available) and genetic differentiation (F_{ST}), that is Isolation by Distance was investigated using linear regression analysis and using genetic distance (F_{ST}/(1–F_{ST})) as the response variable (Rousset, 1997). This approach is a preferred over a Mantel test (Legendre & Fortin, 2010). The relationship between genetic differentiation (F_{ST}) and modelled percentage connectivity was investigated using linear regression. Connectivity between pairs of sites was bidirectional and we used the mean connectivity between each pair of sites for each scenario in the regression. Both the response variable (F_{ST}) and the covariate (percentage oceanographic connectivity) were natural log transformed due to the exponential relationship observed. For this transformation, a small non-zero value was added to the oceanographic connectivity, appropriate since our analysis explores the relative, rather than absolute, values between pairwise comparisons. This was carried out for all seasonal/annual scenarios simulated and Akaike Information Criterion (AIC) was used to infer which scenario or model fitted best with the genetic data. Pseudo-R^2 values (McFadden and Nagelkerke) for the deviance explained by the model were calculated. The relationship between the probability of significant genetic differentiation and mean modelled connectivity was investigated using a generalised linear model with Bernoulli distribution and a logit link. All regression analyses were performed in R V3.5.1 base package (R Development Core Team, 2018). For all analyses, model assumptions were checked visually; scatter plots of standardised residuals against fitted values were used to assess homogeneity of variance; Q-Q plots were used to assess normality; plots of residuals against covariates were used to assess model fit (Zuur et al., 2010).

3 | RESULTS

3.1 | Population genetic structure

A full genetic analysis, including Hardy–Weinberg Equilibrium, linkage disequilibrium and null allele investigation is shown in supplementary material. Genetic results that are of direct interest to the hydrodynamic modelling and associated analyses are described here. Norway was located furthest away from any other population and showed the largest F_{ST} values, all of which were significant (Table 1). Baie de Seine, North Cornwall and Cardigan Bay also showed similarly large F_{ST} values (averaging above 0.3 for all pairwise comparisons) with more than 80% of these being significant. North Cornwall was located on the opposite side of a large peninsula (southwest Britain) from the nearest sampling location, whilst Cardigan Bay and Baie de Seine were in large bays. Populations around the Isle of Man (IOM) were only several kilometres apart and showed low F_{ST} values and/or non-significant values for pairwise comparisons between IOM populations. Populations in the English Channel were up to 100 km apart and generally showed low or non-significant genetic structure with each other apart from three sites that were more isolated: Falmouth, West Falmouth Bay, Baie de Seine (Figure 2). See Appendix S1 for genetic data quality results and loci characteristics. The power analysis found that our suite of microsatellite markers had a power of 0.92 to detect an F_{ST} of 0.001, this fell to a power of 0.81 with an F_{ST} of 0.0009 and 0.5 with an F_{ST} 0.0005. The probability of falsely rejecting genetic homogeneity was 0.08, slightly above a 0.05 cut-off but not considerably larger.

3.2 | Biophysical modelling

Our modelling results showed that a sub-population with high levels of inter-connectivity was produced surrounding the Isle of Man (Sites 1–7), for example Figure 3 showing dispersal from Targets (Site 3) (see also Figure S3_A1-A7). We define sub-populations as groups of sites that are connected with one another in both directions, considering all simulations. One-way connectivity *to* this Isle of Man sub-population *from* surrounding populations (Liverpool, Llyn, Rathlin and Mulroy Bay) was also predicted (Figure S3_A8-A10 and A26-A27). Hence, the Isle of Man is potentially a sink for larval settlement. A second sub-population was simulated for southwest Britain (Sites 13–18), with connectivity mainly directed from east-to-west, for example Figure 4 showing dispersal from Mid Falmouth Bay (Site 16) (see also Figure S3_A14-A17). Other sub-populations were simulated, albeit less well defined: in the central Irish Sea, connecting Cardigan Bay to Tuskar populations (Figure S3_A11); and in the eastern English Channel (west-to-east connectivity between East Channel and Sussex Inshore grounds) (Figure S3_A19-A21). These sub-populations are shown through connectivity networks (Figure 5) and in more detail in the connectivity matrices (Figure 6). Away from these sub-populations, scallop grounds were predicted to be isolated, although often with high levels of local retention (Figure 5).

We simulated spawning over different seasons (April, July and September) and this had considerable implications for dispersal in some cases. Highest levels of connectivity were generally predicted during July, compared to April and September, especially for the Isle of Man sub-population (Figures 5 and 6). Particles released from the Isle of Man grounds tended to disperse less far (and mainly eastwards) during April, in accordance with the typical tidal and wind-driven residuals during spring. During July and September, a change in residual circulation due to summer heating caused particles to disperse further; often northwards or westwards as they became entrained within the western Irish Sea gyre (Figure 3 and S3_A1.1-A1.7). For some other Irish Sea populations, larvae tended to travel further northwards during July and September, than during April (Figure S3_A1.1-A1.13). For Cardigan Bay populations, this seasonality determined whether larvae travelled west to Irish grounds

TABLE 1 Pairwise F_{ST} (above diagonal) and associated p-values (below diagonal)

BDS		**0.040**	0.010	**0.042**	**0.028**	**0.042**	**0.025**	**0.050**	**0.043**	**0.040**	**0.044**	**0.015**	**0.029**
BRO	**.001**		**0.040**	0.008	0.008	0.007	**0.013**	**0.013**	0.004	0.008	0.005	**0.018**	0.008
CDB	.196	**.001**		**0.038**	**0.027**	**0.041**	**0.019**	**0.050**	**0.037**	**0.037**	**0.040**	0.010	**0.026**
CHK	**.001**	.343	**.001**		0.008	0.009	0.009	**0.014**	0.008	0.008	0.009	**0.021**	0.009
ECH	**.001**	.415	**.001**	.467		0.012	0.009	**0.017**	0.008	0.010	0.011	**0.014**	0.007
EDG	**.001**	.415	**.001**	.111	.051		**0.013**	**0.019**	0.009	0.005	0.005	**0.020**	0.009
ELY	**.001**	**.006**	**.001**	**.100**	.334	**.001**		**0.015**	0.011	0.010	**0.014**	0.009	0.006
FAL	**.001**	**.017**	**.001**	**.009**	**.003**	**.001**	**.004**		**0.013**	**0.016**	**0.021**	**0.029**	**0.014**
IOS	**.001**	.926	**.001**	.265	.446	.128	.037	**.021**		0.007	0.008	**0.019**	0.006
IRE	**.001**	.294	**.001**	.217	.160	.909	.054	**.002**	.315		0.008	**0.019**	0.009
LAX	**.001**	.809	**.001**	.194	.133	.799	**.002**	**.001**	.266	.349		**0.020**	0.010
LVB	**.006**	**.001**	.118	**.001**	**.021**	**.001**	.151	**.001**	**.001**	**.001**	**.001**		0.012
MFL	**.001**	.340	**.001**	.174	.603	.105	.593	.011	.631	.184	.092	.035	
MLB	**.001**	.049	**.001**	**.004**	**.019**	**.012**	**.003**	**.001**	.040	.110	.029	**.001**	.073
NCW	.227	**.001**	.155	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.014**	**.001**
NES	**.001**	.774	**.001**	.879	.191	.046	.061	.087	.674	.254	.146	**.001**	.137
NOR	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**
PEL	**.001**	.303	**.001**	.185	.256	.277	**.022**	**.002**	.842	.561	.587	**.001**	.293
PSM	**.001**	.132	**.001**	**.009**	**.004**	**.019**	**.002**	**.017**	.031	.308	**.018**	**.001**	**.013**
SES	**.001**	.377	**.001**	.593	.246	.651	.146	**.003**	.340	.957	.503	**.002**	.555
SXI	**.001**	.490	**.001**	.145	.243	.152	.028	**.007**	.239	.518	.097	**.001**	.154
TAR	**.001**	.984	**.001**	.624	.741	.662	.030	**.014**	.843	.929	.867	**.002**	.258
WFL	.214	**.001**	.477	**.001**	**.002**	**.001**	.031	**.001**	**.001**	**.001**	**.001**	.314	**.001**
WLY	**.001**	.37	**.001**	.394	.893	.198	.5	**.001**	.306	.285	.15	.052	.862

Note: p-values and F_{ST} values in bold are significant following correction for multiple testing using the False Discovery Rate (Benjamini & Hochberg, 1995). Please see Figure 1 for site abbreviations. Colour coding of F_{ST} values: white = non-significant, grey = significant. Colour coding of sites: white = Irish Sea, light grey = English Channel, dark grey = wider shelf.

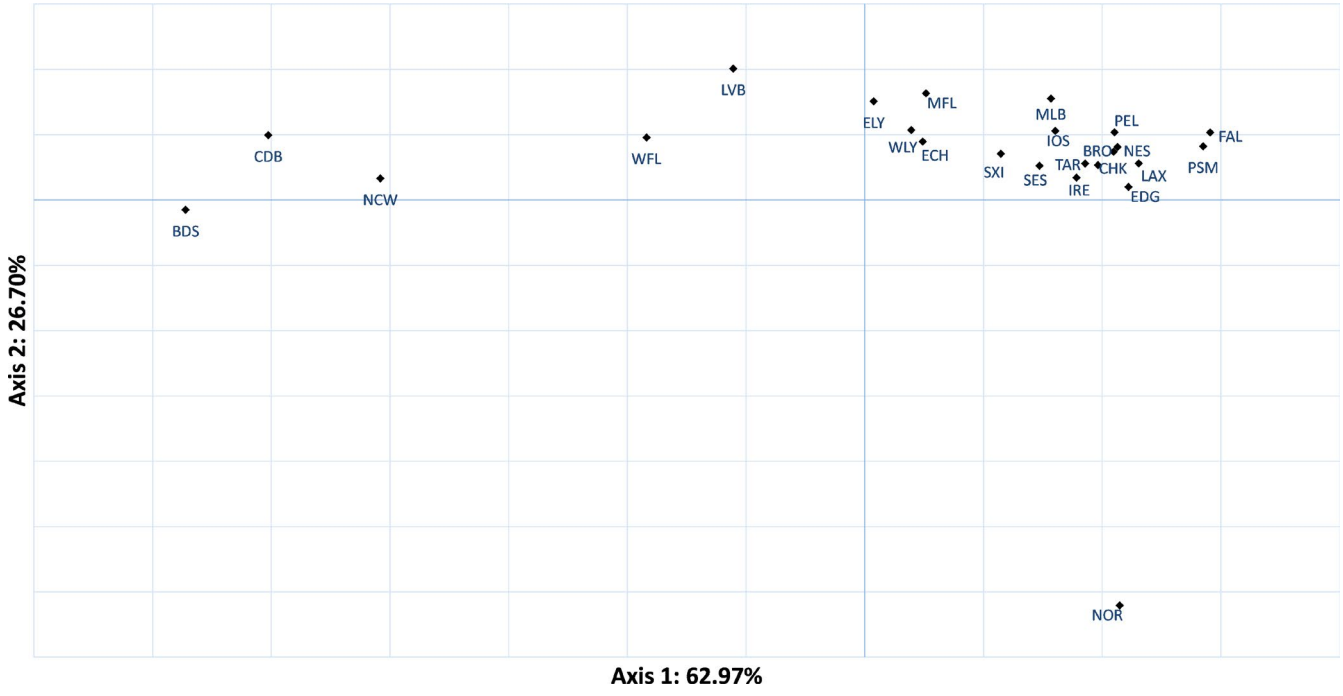

FIGURE 2 Principle coordinate analysis illustrating the sites contributing to genetic differentiation from microsatellite analysis. (Site codes see Figure 1)

0.041	0.010	**0.043**	**0.054**	**0.045**	**0.051**	**0.036**	**0.034**	**0.040**	0.010	**0.028**
0.011	**0.038**	0.005	**0.031**	0.008	0.010	0.007	0.007	0.004	**0.025**	0.009
0.040	0.010	**0.039**	**0.057**	**0.040**	**0.048**	**0.033**	**0.033**	**0.037**	0.007	**0.025**
0.014	**0.039**	0.005	**0.032**	0.009	**0.013**	0.006	0.009	0.006	**0.026**	0.008
0.014	**0.028**	0.010	**0.032**	0.010	**0.018**	0.009	0.009	0.006	**0.019**	0.006
0.013	**0.039**	0.010	**0.027**	0.008	**0.013**	0.006	0.009	0.006	**0.028**	0.010
0.016	**0.020**	0.010	**0.036**	**0.012**	**0.016**	0.008	0.011	0.010	0.012	0.008
0.021	**0.045**	0.010	**0.043**	**0.018**	**0.014**	**0.015**	**0.014**	**0.013**	**0.033**	**0.019**
0.011	**0.037**	0.006	**0.035**	0.005	0.012	0.007	0.008	0.005	**0.025**	0.009
0.010	**0.037**	0.008	**0.026**	0.007	0.008	0.004	0.007	0.004	**0.026**	0.009
0.013	**0.042**	0.009	**0.033**	0.007	**0.014**	0.007	0.010	0.005	**0.029**	0.011
0.021	**0.013**	**0.021**	**0.042**	**0.020**	**0.025**	**0.016**	0.016	0.018	0.009	0.013
0.011	**0.028**	0.009	**0.038**	0.008	**0.014**	0.006	0.009	0.008	**0.017**	0.006
	0.035	**0.014**	**0.040**	0.008	**0.014**	**0.012**	**0.013**	0.010	**0.030**	**0.015**
.001		**0.039**	**0.053**	**0.037**	**0.049**	**0.036**	0.032	**0.036**	0.008	**0.027**
.005	**.001**		**0.034**	0.009	0.008	0.006	0.006	0.004	**0.025**	0.010
.001	**.001**	**.001**		**0.035**	**0.038**	**0.028**	**0.029**	**0.029**	**0.045**	**0.036**
.299	**.001**	.151	**.001**		**0.015**	0.007	0.010	0.006	**0.028**	0.011
.011	**.001**	.323	**.001**	**.009**		0.007	0.009	0.009	**0.034**	**0.018**
.019	**.001**	.525	**.001**	.388	.420		0.005	0.004	**0.021**	0.009
.011	**.001**	.535	**.001**	.077	.242	.727		0.005	**0.020**	0.011
.044	**.001**	.894	**.001**	.556	.161	.902	.754		**0.025**	0.009
.001	.380	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**	**.001**		**0.018**
.012	**.001**	.107	**.001**	.111	**.003**	.244	.116	.314	**.004**	

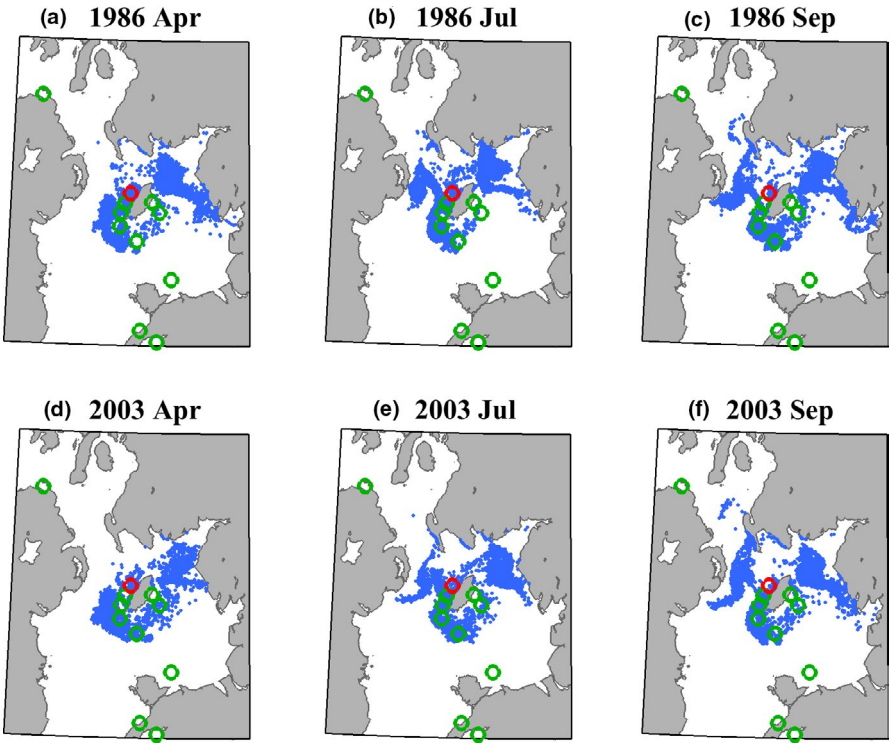

FIGURE 3 Panels show final locations (blue pixels) for 100,000 particles released from the site 'Targets' (Site 3; red circle) on the dates indicated. Green circles denote surrounding scallop release sites. Panels display variability on seasonal timescales (columns), and inter-annual variability (rows). Particle Tracking Model output from other release locations are presented in the Appendices S1 and S2

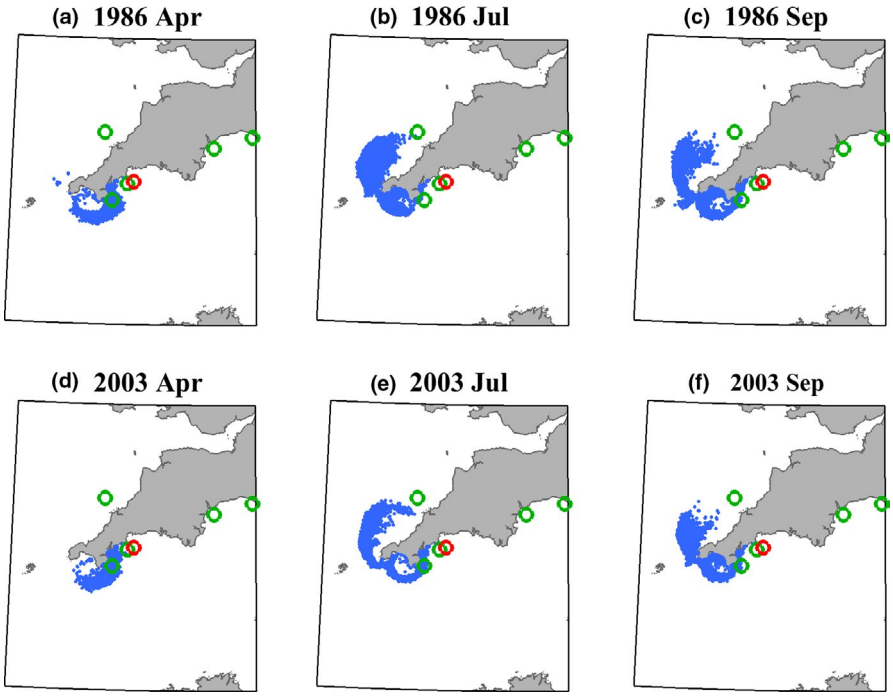

FIGURE 4 Panels show final locations for 100,000 particles released from Mid Falmouth Bay (Site 16; red circle) on the dates indicated. Green circles show neighbouring sites. Panels a-f display seasonal (columns) and inter-annual (rows) variability. Particle Tracking Model output from other release locations are presented in the Appendices S1 and S2

(Tuskar) or north towards Tremadog (Figure S3_A1.11). Simulated dispersal in the English Channel varied seasonally with connectivity between populations that are 50–100 km apart only possible in selected months—usually July or September (for example between West Falmouth and Mid Falmouth) (Figure S3_A1.14-A1.21). For northern Britain, particles dispersed further south during the latter release months (Figure S3_A1.22, S3_A1.24 and A1.25). During the warmer year (2003), simulated larvae tended to travel further on average (+3%), with increased connectivity (+13%) and increased retention (+9%), compared with the cold year (1986) (Figure 7)—in effect, the warm year appeared to 'streamline' the larvae, which is potentially why connectivity, retention and distance all increased. The increased local retention in 2003, however, was mainly due to changes for a few sites off the western coast of the Isle of Man (Sites 4–6), where retention increased during July 2003, possibly due to a shift in the position of the Western Irish Sea gyre and Irish Sea front.

Considering all simulated populations, larvae were generally predicted to disperse within 100 km (c. 54 nautical miles) of their release location after 50 days PLD (Figure 7), suggesting that stepping-stone connectivity via intermediary sites would be necessary to connect the entire meta-population. Indeed, the outlying North Sea and Atlantic coast populations (Sites 22–25 and 28) did not settle elsewhere due to their geographic isolation (Figure 5). Retention was also relatively low (<10%) for sites in exposed and tidally energetic locations (e.g. North Cornwall, SE Scotland and NE Scotland) (Figure 6).

3.3 | Drivers of genetic differentiation

The linear model used to investigate Isolation by Distance (IBD) was not consistent at different spatial scales (Figure 8a). Significant IBD was shown at the scale of the Irish Sea, R^2 (adjusted) = 0.601 ($F_{1,43}$ = 67.21, p < .0001) (Figure 8b). The residual plots at the scale of the Irish Sea showed a non-linear pattern in the standardised residuals, suggesting that oceanographic distance by itself was not satisfactory to model genetic differentiation. No IBD was seen in the English Channel ($F_{1,29}$ = 0.1509, p = .701). At the northwest European shelf scale, there was a significant IBD but with a low R^2 (adjusted) of 0.128 ($F_{1,198}$= 30.11, p < .0001) and, again, possible non-linear patterns in the standardised residual plots.

The relationship between modelled connectivity and F_{ST} varied depending on the scale or sea basin used. There was a significant relationship when looking at the whole data set, however, the R^2 (adjusted) values were low (Table 2) showing that the overall relationship is weak. The linear regression of ln(F_{ST}) and ln(modelled percentage connectivity) in the English Channel was not significant in any of the six release scenarios (Table 2). However, there was a significant negative relationship between genetic differentiation and modelled connectivity within the Irish Sea/Celtic Sea basin (Figure 9). Within the Irish Sea, there was limited development of genetic structure above 5% connectivity, below which there was a rapid increase in the upper bound of F_{ST}. However, there were instances of low F_{ST} with zero modelled connectivity creating a highly heteroskedastic relationship. The residual plots for connectivity and F_{ST} in the Irish Sea were an improvement on the IBD plots with homogeneity of variance demonstrated. The relationship when looking at sites between different sea basins could not be modelled as there was no connectivity simulated between any site pairs across sea basins.

The generalised linear model analysing the relationship between modelled connectivity and the proportion of F_{ST} estimates differing significantly from zero was not significant for any release dates in the English Channel or wider spatial scales. In the Irish Sea, however, the relationship was significant at all release dates and model scenarios via AIC preferred the April 2003 release date. The likelihood of

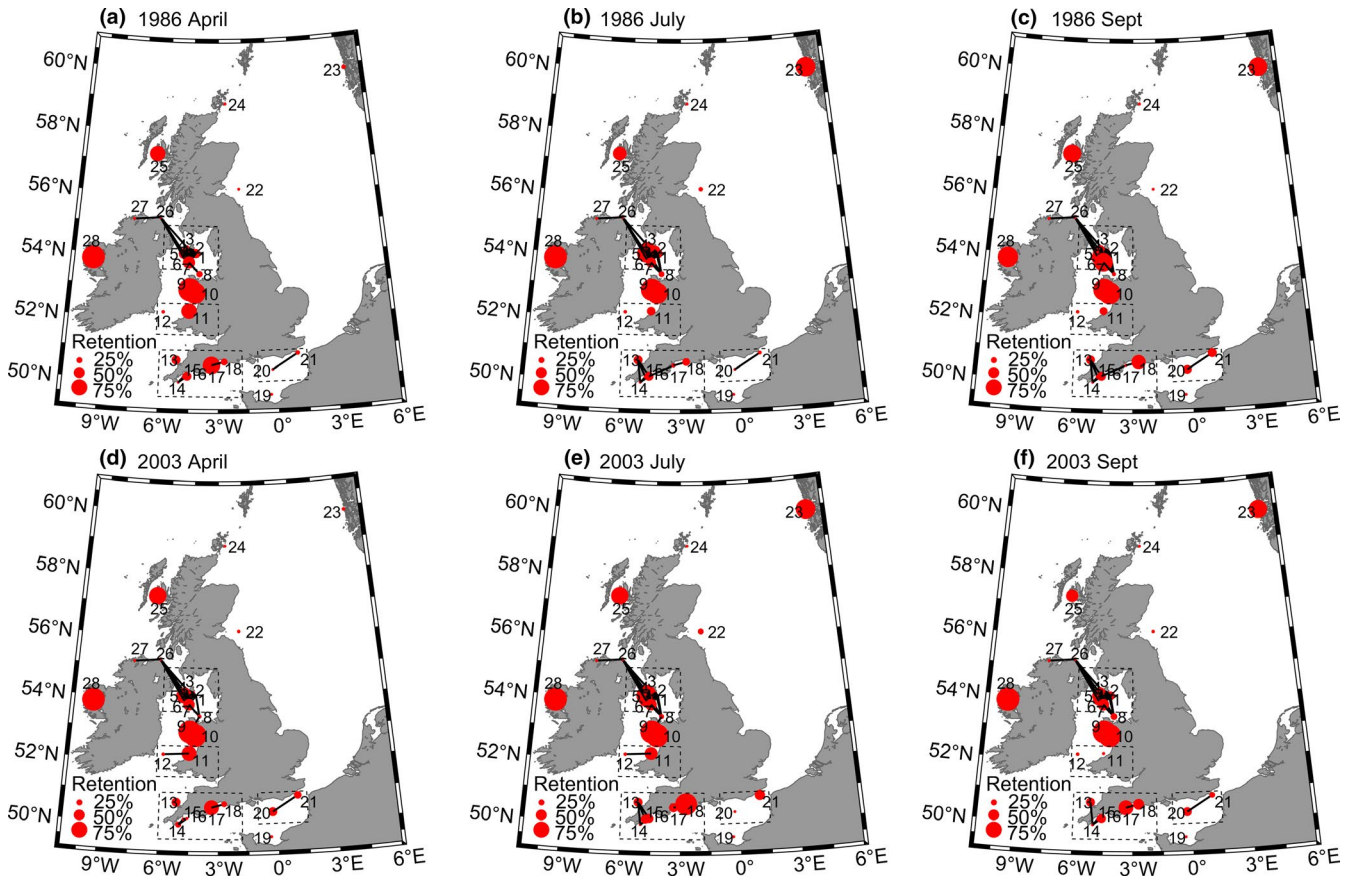

FIGURE 5 (a–f) Simulated connectivity probability maps for 28 scallop populations within the northwest European shelf seas, based on 30–50-day Pelagic Larval Duration for larval release dates (a) 01–05 April 1986, (b) 01–05 July 1986, and (c) 01–05 September 1986 (d) 01–05 April 2003, (e) 01–05 July 2003, and (f) 01–05 September 2003. The size of the red circles indicates the level of larval retention. Black lines show larval connectivity between populations. Connectivities may be one-way, or two-ways; see Figure 6. Dotted boxed denote sub-populations identified

significant genetic differentiation declined rapidly between 0% and 5% percentage connectivity above which there was no significant genetic differentiation predicted (Figure 10). The deviance explained was 40% and pseudo-R^2 values ranged from 0.41 (McFadden) to 0.57 (Nagelkerke). The 95% confidence intervals show that the prediction of no significant genetic differentiation above 5% connectivity is likely to be very accurate.

4 | DISCUSSION

Our results provide valuable insights into the scale at which connectivity and population structuring occurs for scallop and other species with discrete aggregations/distributions and adds to the understanding of the complex determinants of connectivity in broadcast-spawning organisms with prolonged larval duration. Genetic data suggested broad-scale homogeneity in microsatellite alleles with patchy significant differentiation associated with specific sites, often within bays. Modelling estimated discrete populations of scallops to be inter-connected at a basin or meso-scale (~100 km) but with less connectivity within a single generation above this distance, suggesting stepping-stone larval dispersal. This scale of connectivity is similar to a previous study in the English Channel which estimated scallop larvae dispersal distances varied from 13 km up to 90 km (Nicolle et al., 2016). The likelihood of connectivity and retention was predicted to increase for a relatively warm year. Results highlight that the grain of sampling (both spatial and temporal) is an important consideration that reflects the multigenerational connectivity potential to characterise the meta-population structure, and thereby inform marine management.

4.1 | Population genetics

Broad-scale genetic homogeneity with patchy differentiation of some distant or bay sites is in line with the previous studies using allozymes (Beaumont et al., 1993; Ridgway et al., 2000), RAPD (Wilding et al., 1997), mitochondrial markers (Heipel et al., 1998) and microsatellites (Morvezen et al 2016). Handal et al. (2020) found some weak significant differentiation between samples from south west England with the eastern channel and the coast of France. However, only two pairwise comparison remained significant after

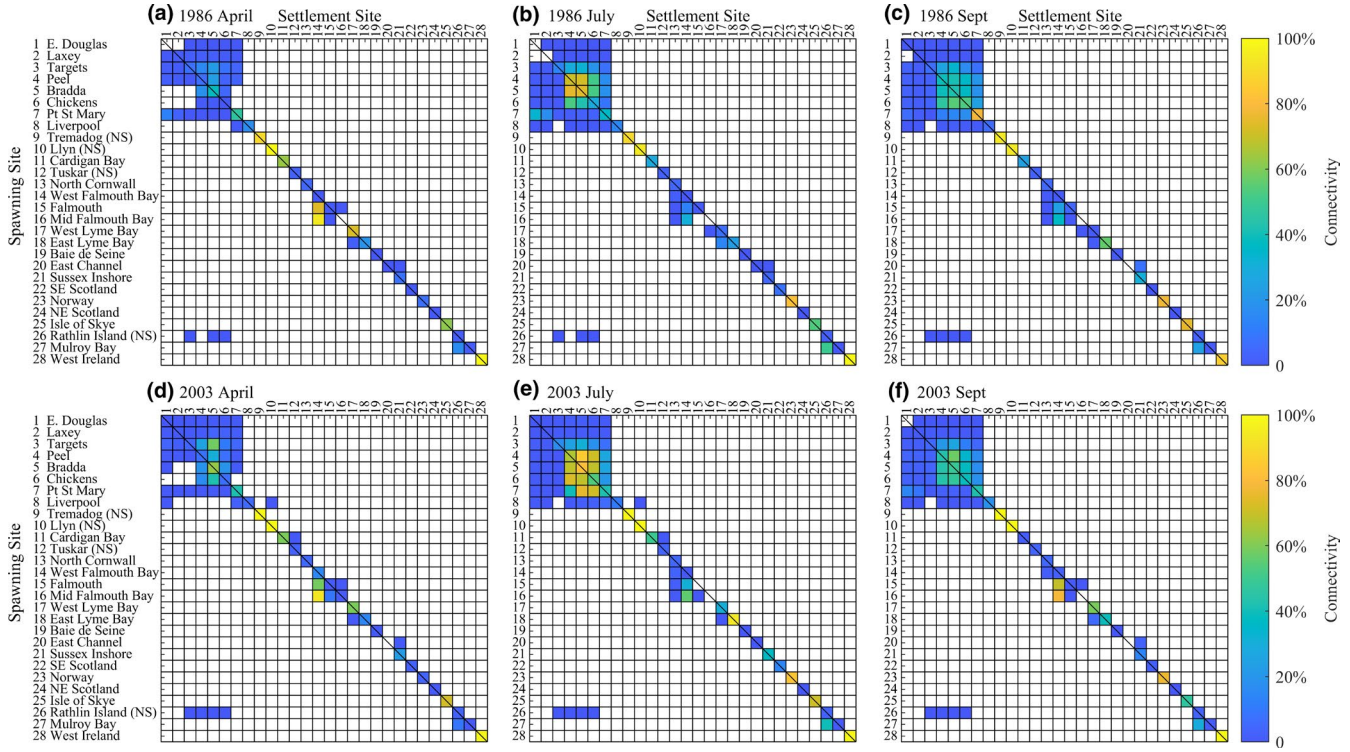

FIGURE 6 Connectivity matrices, showing simulated probability of larval retention and connectivity for larval release dates (a) 01–05 April 1986, (b) 01–05 July 1986, (c) 01–05 September 1986, (d) 01–05 April 2003, (e) 01–05 July 2003, and (f) 01–05 September 2003. Larval retention is shown in the diagonal cells. Larval connectivity is off diagonal. White cells indicate no connectivity

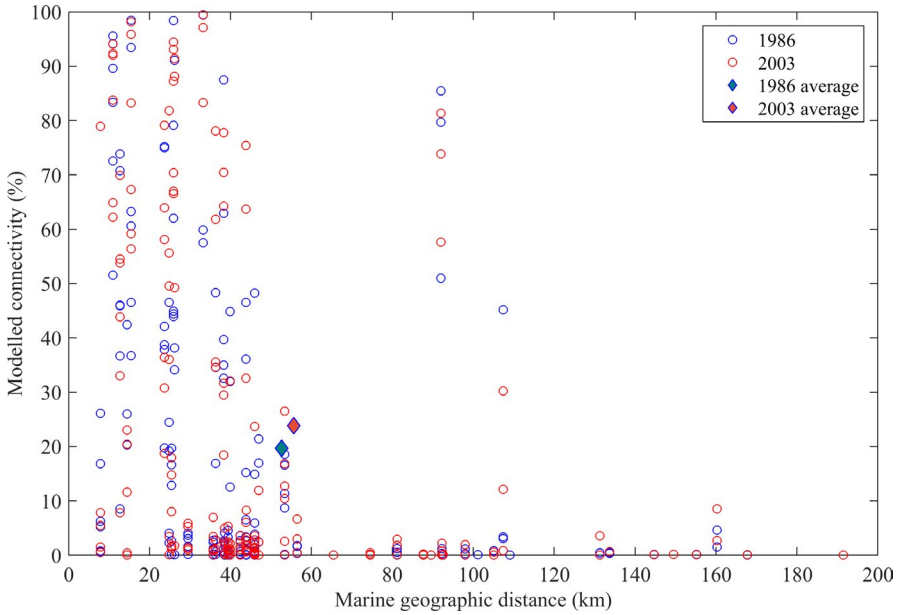

FIGURE 7 Relationship between modelled connectivity and oceanographic distance showing the difference between a warm year (2003) and a cold year (1986). Most simulations resulted in less than 100 km dispersal

correction for multiple testing showing similarity with the current results. Our results suggest that significant genetic differentiation occurs primarily at modelled connectivity values of 5% or lower, consistent with population genetics theory (Crow & Kimura, 2009). Such low levels of migration are probably not substantial enough to influence population dynamics as the shift between demographic independence and dependence is estimated to occur with migration in excess of 10% (Hastings 1993), therefore, in temporally stable populations, pairwise sites with significant genetic differentiation should be interpreted as demographically independent populations when considering spatial conservation and management solutions. However, several neutral demographic processes can generate chaotic genetic patchiness: sweepstakes reproductive success and collective dispersal (Eldon et al., 2016). In this study, the age structure

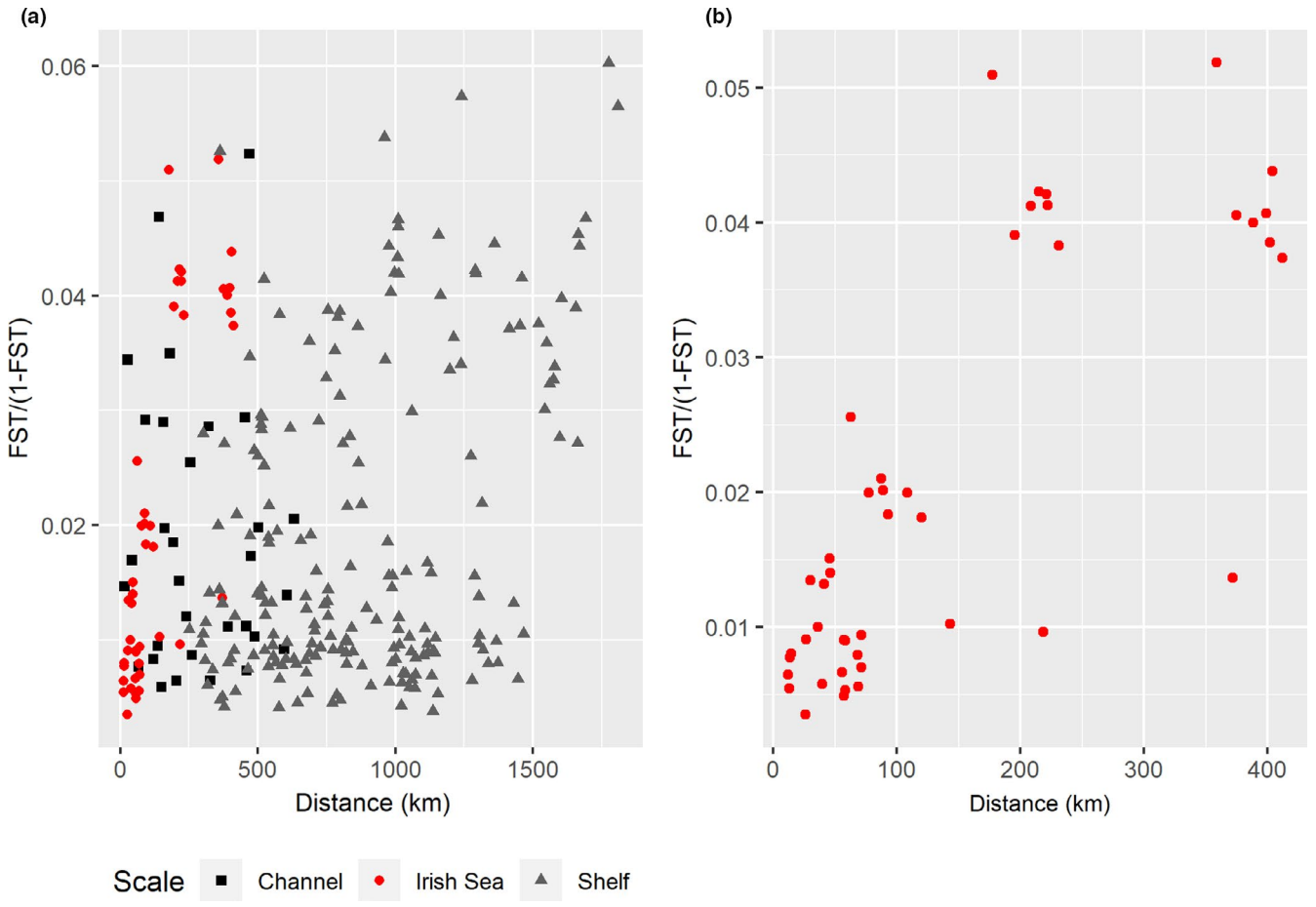

FIGURE 8 Isolation by distance: $F_{ST}/(1-F_{ST})$ with oceanographic distance; (a) all sites (b) Irish Sea/Celtic Sea sites only

of the samples varied between sites. Some sites were dominated by one or two age groups whilst others had a broad range of ages represented. Temporal variation in reproductive success can cause different cohorts to be genetically differentiated. This may be a key factor in some populations in this study that show uncharacteristically large F_{ST} values, such as those from Baie de Seine or Cardigan Bay. The results from Baie de Seine in this study are different to those from (Handal et al., 2020). The scallop samples in Handal et al. (2020) were harvested from slightly further east than in present study but also were from a different cohort, possibly showing some spatial variation or temporal genetic structure.

The presence of some pairwise populations with non-significant genetic differentiation with less than 5% connectivity (zero in some cases) could be due to (1) large effective population size (Ne) combined with short evolutionary time since de-glaciation decreasing the divergence from shared ancestral population frequencies; (2) stepping-stone recruitment where two populations that are not directly connected are able to share genes via an intermediate population. For example, genetic data suggest that the sites off the west coast of Scotland are connected to some sites around the Isle of Man and the English Channel. It is unlikely that this represents present-day connectivity on an ecologically important scale; rather, that larger Ne's have not experienced enough generations for divergence to occur or limited stepping-stone recruitment over many generations has been able to homogenise allele frequencies.

4.2 | Biophysical modelling

Recorded scallop fishing effort along the English Channel (Figure S4) suggests that the scallop grounds are almost continuous inshore along the English coast which would allow stepping-stone dispersal/connectivity over several successive generations (Robins et al., 2017). In this study, dispersal simulations were within a few kilometres of predicting 'connectivity' between West Lyme Bay and Mid Falmouth Bay, and between East Lyme Bay and East Channel (Figure S1.17 and A1.18). Hence, it seems plausible given favourable conditions (e.g. strong winds, stronger residual currents) that those English Channel populations could be connected in one generation. This is seen in the results of ocean modelling by Nicolle et al. (2016), which used much larger fishing grounds as the available settlement for particles compared to our smaller 10 km radius settle zones (more representative of beds). They showed high local retention within many grounds, including Baie de Seine and greater connectivity. However, this appears to be driven by the differences in the

TABLE 2 Parameter estimates for the linear model for (ln-ln transformed) genetic differentiation (F_{ST}) and modelled connectivity (%) at different simulated spawning dates

Scale	Year	Month	Coefficient	Estimate	*SE*	*t*	*P*	*F*	*df*	*P*	Adjusted R^2
Irish sea	1986	April	Intercept	−4.67907	0.10207	−45.843	<.00001	56.38	1,43	***<.00001***	0.56
			Ln Connectivity	−0.16815	−0.02239	−7.509	<.00001				
		July	Intercept	−4.45491	0.09258	−48.118	<.00001	43.75		***<.00001***	0.49
			Ln Connectivity	−0.14291	0.02161	−6.614	<.00001				
		September	Intercept	−4.43895	0.0841	−52.782	<.00001	57.42		***<.00001***	0.56
			Ln Connectivity	−0.15143	0.01998	−7.578	<.00001				
	2003	April	Intercept	−4.61861	0.08566	−53.919	<.00001	78.62		***<.00001***	0.64
			Ln Connectivity	−0.17114	0.0193	−8.867	<.00001				
		July	Intercept	−4.41378	0.09356	−47.176	<.00001	38.08		***<.00001***	0.46
			Ln Connectivity	−0.13529	0.02192	−6.171	<.00001				
		September	Intercept	−4.4842	0.08466	−52.964	<.00001	61.7		***<.00001***	0.58
			Ln Connectivity	−0.15104	0.01923	−7.855	<.00001				
Total	1986	April	Intercept	−4.56415	0.11735	−38.895	<.00001	10.49	1,274	***.0013***	0.033
			Ln Connectivity	−0.06618	0.02044	−3.239	.00135				
		July	Intercept	−4.4648	0.09976	−44.756	<.00001	7.985		***.0051***	0.025
			Ln Connectivity	−0.04966	0.01757	−2.826	.00506				
		September	Intercept	−4.48323	0.09664	−46.391	<.00001	9.894		***.0018***	0.031
			Ln Connectivity	−0.05371	0.01708	−3.146	.0018				
	2003	April	Intercept	−4.55878	0.10794	−42.235	<.00001	12.33		***.0005***	0.04
			Ln Connectivity	−0.0662	0.01886	−3.511	.0005				
		July	Intercept	−4.43238	0.09753	−45.447	<.00001	6.446		***.0117***	0.019
			Ln Connectivity	−0.04353	0.01715	−2.539	.0117				
		September	Intercept	−4.50893	0.09807	−45.978	<.00001	11.4		***.0008***	0.036
			Ln Connectivity	−0.05797	0.01717	−3.377	.00084				
English channel	1986	April	Intercept	−3.9744	0.2161	−18.394	<.00001	1.18	1,29	.2864	0.006
			Ln Connectivity	0.0416	0.0383	1.086	.286				
		July	Intercept	−3.98692	0.20118	−19.818	<.00001	1.26		.2707	0.008
			Ln Connectivity	0.04223	0.0376	1.123	.271				
		September	Intercept	−4.06776	0.19939	−20.401	<.00001	0.43		.5149	−0.019
			Ln Connectivity	0.02492	0.03779	0.659	.515				
	2003	April	Intercept	−4.04579	0.20309	−19.92	<.00001	0.59		.4476	−0.013
			Ln Connectivity	0.02784	0.03616	0.77	.448				
		July	Intercept	−3.917	0.19962	−19.62	<.00001	2.372		.1344	0.043
			Ln Connectivity	0.05611	0.03643	1.54	.134				
		September	Intercept	−4.10263	0.19362	−21.19	<.00001	0.222		.6413	−0.027
			Ln Connectivity	0.01644	0.03492	0.471	.641				

Note: Bold italics indicate models with *p*-values < 0.05.

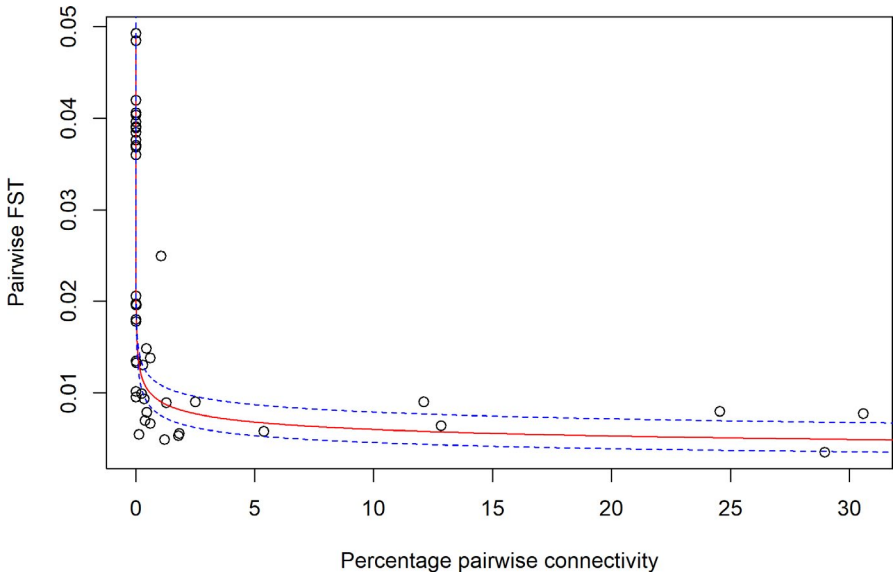

FIGURE 9 Pairwise genetic differentiation (F_{ST}) and modelled percentage pairwise connectivity in the Irish Sea. Solid red line = fitted values, dotted blue lines = 95% confidence intervals

size of the settlement zones as their average particle tracks are very similar to the present study.

The oceanographic connectivity predicted by our model showed large temporal variation both over timescales of days and over seasonal and inter-annual time scales. The timing of larvae release had a significant influence on connectivity and the direction of larval transport which highlights the importance of understanding spawning and larval behaviour to inform model parameters. This presents a major knowledge gap across a broad range of species. A warmer year resulted in higher levels of modelled connectivity than a cold year. It is thought that the onset of spawning in scallops is influenced by changing temperature (e.g. Hold et al., 2013), therefore, the variability of connectivity with timing of spawning has important implications for seawater warming and its possible alterations to recruitment patterns. Seasonally, within the Irish Sea, in both warm and cold years the modelled connectivity in April and September more closely aligned with genetic data for scallops than the July release dates, with an April release in a warm year showing the best alignment with genetic data and this fits with the spring and autumn spawning peaks described for this region (Brand et al., 1980; Mason, 1958). Summer spawning species may show greater dispersal distances than species that spawn during the spring or autumn. Spawning dates will also affect the direction of larval transport. Thus, species and location-specific information is required when using models for spatial planning of marine protected areas or fisheries management: the connectivity between populations could be grossly over or under estimated if the incorrect spawning time is used. For example, genetic data suggest that Cardigan Bay could be isolated for scallops, but modelled connectivity showed the population acting as a source for Tuskar to the east in spring and summer and acting as a sink for larvae from Llyn and Tremadog Bay in summer/autumn, for example the role of sources and sinks may very periodically. Without consideration of the spawning timing, the modelling results may lead to an over estimation of the connectivity and resilience in this area of Cardigan Bay as there may be no external larval supply from spring spawning. Studies into the reproductive schedules of scallops across much of their range suggest that there is a partial but synchronised spring spawning and a more complete spawning in the autumn with minimal trickle spawning over the summer months (Duncan et al., 2016; Mason, 1958). Settlement studies in the Isle of Man suggest that a major settlement peak occurs following the spring spawning in July with limited settlement detected on artificial spat collectors after the major autumn spawning event (Brand et al., 1980). This is reflected in this study for the Irish Sea results with the greater alignment of the genetic data with the connectivity predicted from April and September release dates compared with July, with the greatest alignment being with April release in a warm year.

The oceanographic model helps explain the probabilistic variability in connectivity with environmental variability, that is ocean heating. Our simulated warm year appeared to 'streamline' the larvae, which is potentially why simulated connectivity, retention and distance all increased. One could infer from our results that projected ocean heating (Lowe et al., 2018) would strengthen connectivity networks and self-recruitment. However, temperature differences between the two years comprise spatio-temporal variability that was averaged out in our study, and may mask other important drivers of connectivity differences, for example changes in wind and wave patterns (e.g. Neill & Hashemi, 2013). Evidently, more work is required to reduce model uncertainties with this regard and also accounting for biophysical responses to ocean warming such as reduced PLD. If found to be true, this study has implications for population resilience to over-exploitation (e.g. see Shephard et al., 2009).

4.3 | Application to conservation management

The results of our study suggest that the microsatellite genetic data used in this study can only be used as a guide to the largest scale for spatial management: the presence of genetic structure will relate to

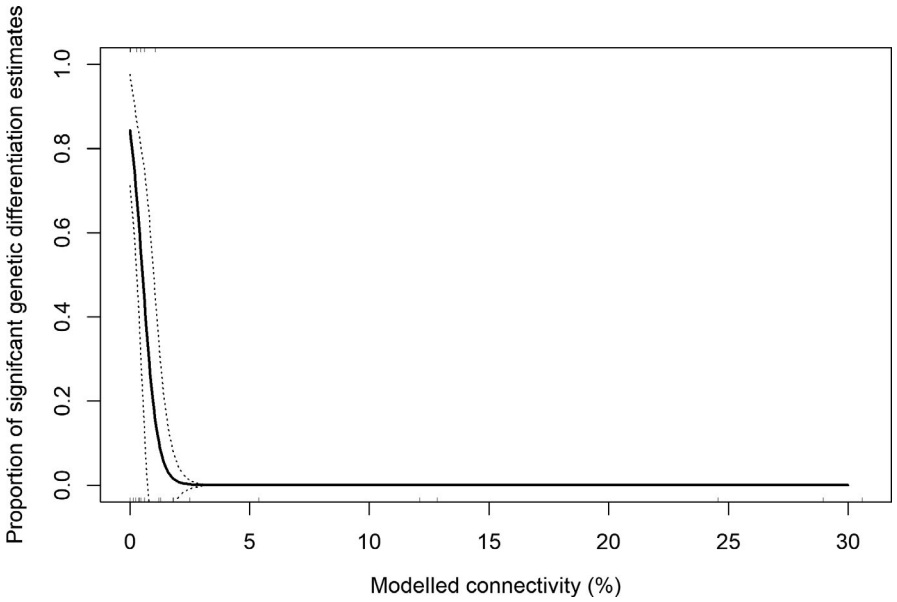

FIGURE 10 Generalised linear model (Bernouli distribution) of proportion of significant genetic differentiation estimates (F_{ST}) with modelled percentage connectivity in the Irish Sea. Solid line = fitted values; dotted lines = 95% confidence intervals

demographic independence (<5% connectivity), however, a lack of detectable genetic differentiation may not relate to migration levels required for demographic dependence between populations, or be reliant on stepping-stone recruitment. In addition, temporal instability driven through processes such as sweepstake recruitment can drive genetic differentiation patterns rather than genetic isolation.

Within the Irish Sea, genetic data suggest that scallop stocks around the Isle of Man (IOM) are connected, whilst Cardigan Bay, Liverpool Bay, North Cornwall and Mulroy Bay appear to be largely isolated. Using insight from the larval dispersal model, we can see that for some IOM populations the probability of larval exchange was less than 10% per spawning event which could be high enough for populations to maintain genetic connectivity but may not be sufficient for populations to rapidly recover via immigration if over-exploited, rather being reliant on multigenerational recruitment through intermediary sites. Hence, recovery from over-exploitation is possible albeit with varying timing depending on the reliance on multigenerational connectivity. Fishery management plans should be robust to this possible low levels of external recruitment that could otherwise lead to slower rates of recovery from over-fishing (e.g. Gimenez et al., 2019) by ensuring that local brood stocks are maintained at sufficient levels to allow self-sufficient recruitment. In addition, the results suggest that single meta-population approaches to spatial management may be inappropriate in some locations. For example, modelled connectivity showed some connectivity within the eastern channel and within the western channel, in line with that modelled previously (Nicolle et al., 2016), suggesting that a regional approach to scallop fishery management is required to ensure sustainable practices. This study shows that for successful spatial management exact boundaries between stocks need to be simulated accurately by including all intermediary sites and multigenerational stepping-stone dispersal.

This potential for regional separation and some individual site isolation has implications for the management of exploited populations showing that a biophysical larval dispersal model, coupled with good biological data can provide an important tool for evidence-based management. Conversely, care needs to be taken with genetic data due to the low levels of connectivity needed to homogenise allele frequencies and the potential for temporal instability to drive differentiation rather than isolation.

5 | CONCLUSION

Connectivity of king scallop at the scale of the European shelf seas is low, but within sea basins are generally high. Localised currents within sea basins can decrease connectivity to form isolated populations that would be overlooked when using distance-based methods alone. The grain of sampling and the scale at which modelling are conducted greatly influences the accuracy of the outputs, and it is recommended that when sampled sites are greater than 100 km apart stepping-stone recruitment via intermediate sites should be considered. The study also highlights the potential for variation in annual sea temperature and associated environmental factors to drive variation in connectivity and recruitment. Further investigation is needed to elucidate this relationship and its possible implications for future warming oceans. Finally, this study demonstrates the value of using oceanographic modelling to inform management of marine species.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTION

NH, PR and MJK were involved in conception and design of methodology. NH, PR, CLS, GL, HL, MK and EB were involved in the acquisition of data. NH, PR and GL were involved in data analysis. NH, PR and MJK led the writing of the article. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The microsatellite data along with the site location data that support the findings of this study are openly available in FigShare at https://figshare.com/account/articles/12907430 https://doi.org/10.6084/m9.figshare.12907430.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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